Chiton integument: Ultrastructure of the sensory hairs of *Mopalia muscosa* (Mollusca: Polyplacophora)

By: Esther M. Leise and Richard A. Cloney

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Summary:
The dorsal integument of the girdle of the chiton *Mopalia muscosa* is covered by a chitinous cuticle about 0.1 mm in thickness. Within the cuticle are fusiform spicules composed of a central mass of pigment granules surrounded by a layer of calcium carbonate crystals. Tapered, curved chitinous hairs with a groove on the mesial surface pass through the cuticle and protrude above the surface. The spicules are produced by specialized groups of epidermal cells called spiniferous papillae and the hairs are produced by trichogenous papillae. Processes of pigment cells containing green granules are scattered among the cells of each type of papilla and among the common epidermal cells.

The wall or cortex of each hair is composed of two layers. The cortex surrounds a central medulla that contains matrix material of low density and from 1 to 20 axial bundles of dendrites. The number of bundles within the medulla varies with the size of the hair. Each bundle contains from 1 to 25 dendrites ensheathed by processes of supporting cells. The dendrites and supporting sheath arise from epidermal cells of the central part of the papilla. At the base of each trichogenous papilla are several nerves that pass into the dermis. Two questions remain unresolved. The function of the hairs is unknown, and we have not determined whether the sensory cells are primary sensory neurons or secondary sensory cells.
Key words: Chiton — Integument — Nerves — Sensory hairs — Spicules
Abbreviations. *A* axon; *BL* basal lamina; *C* cuticle; *CC* subcortical cell; *CEC* common epidermal cells; *CO* collagen; *CR* cortical rod; *D* dendrite; *DE* dermis; *G* ovoid granule; *GB* Golgi apparatus; *GR* longitudinal groove; *H* hemidesmosome; *IC* inner cortex; *ID* interdigitation; *L* Y lysosome; *M* mitochondrion; *MC* submedullary cell; *ME* medulla; *MT* microtubules; *MU* muscle fiber; *MV* multivesicular body; *N* nucleus; *NE* nerve; *NS* neurosecretory vesicles; *OC* outer cortex; *P* pigment granules; *RER* rough endoplasmic reticulum; *S* spicule; *SC* supporting cell; *SJ* septate junction; *SP* spiniferous papilla; *T* tonofilaments; *V* microvilli; *VE* vacuole; W artifactual wrinkle; *ZA* zonula adhaerens

Article:

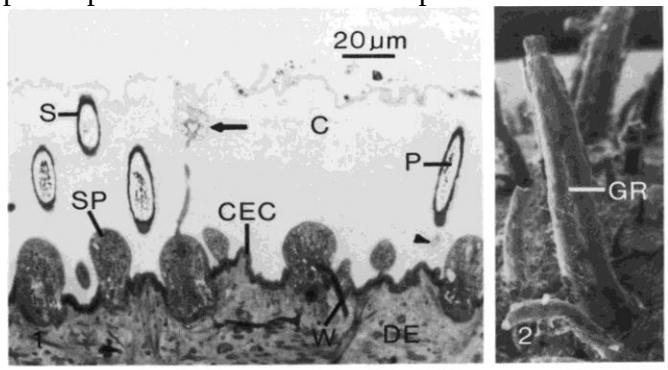
A muscular girdle (perinotum) surrounds the shell plates of all chitons. Structures secreted by the epidermis of the girdle have been described as ornamentation or armature (Hyman 1967), but recent studies suggest that the girdle epidermis has other functions. The spicules of *Lepidochitona cinereus* (Haas and Kriesten 1975) and *Acanthochiton fascicularis* (Fischer et al. 1980) are attached to epidermal papillae which may contain mechanoreceptors. Fischer et al. also suggest that some epidermal cells of *A. fascicularis* are photoreceptors.

Species in the family Mopaliidae and the genus *Chaetopleura* (Chaetopleuridae) have bristles or hairs on the dorsal surface of the girdle (Bergenhayn 1955). The simplest and largest girdle hairs, such as those on *Mopalia muscosa*, are unbranched chitinous processes. The external morphology of the hairs of many species has been described (Leloup 1942) but little is known of their ultrastructure. Many types of hairs, such as those of *Placiphorella* (Mopaliidae) and *Chaetopleura* (Chaetopleuridae), arise from multicellular papillae in epidermal invaginations (Plate 1902), but there have been no reports of cellular structures within the hairs. Our studies of

M. muscosa led to the discovery of nerve fibers within the hairs. In this paper we describe the general organization of the dorsal integument and the fine structure of adult hairs, their innervation and possible functions.

Materials and methods

Adult specimens of *Mopalia muscosa* Gould were collected from Alki Point in Seattle, and from Cattle Point on San Juan Island, Washington, during the spring and summer of 1978 and 1979. They were maintained for as long as 2 months at 10° C in tanks of aerated seawater or on sea-water tables at 10°15° C. They were fed fronds of the brown alga *Nereocystis leutkeana.* Small pieces of the girdle were removed from 12 animals and fixed in a solution containing 2.5% glutaraldehyde, 0.2 M Millonig's phosphate buffer and 0.14 M sodium chloride (pH 7.6, 960 milliosmoles) for 1 h at room temperature. An equal volume of 10% disodium EDTA was then added to specimens that were to be decalcified. These specimens were left in the solution for 5-6 h or overnight. All samples were briefly rinsed in the post-fixation buffer, then post-fixed in a solution of 2% osmium tetroxide and 1.25% sodium bicarbonate (pH 7.4) (Cloney and Florey 1968). The material was rinsed in water, dehydrated in ethanol, transferred through 2 changes of propylene oxide, then infiltrated and embedded in Epon (Luft 1961). The material did not infiltrate well with only 2 changes of the antemedium-Epon mixture. Better results were obtained when 3 infiltration steps were used with propylene oxide: Epon ratios of 2: 1, 1: 1, 1: 3, followed by pure Epon. The total infiltration period was 36 to 48 h.



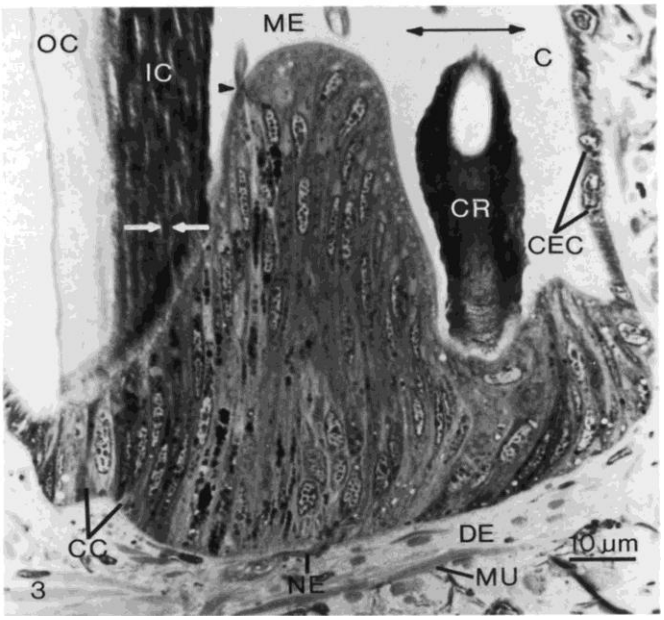


Fig. 1. Longitudinal section through the decalcified integument of *M. muscosa*. Spicules (*S*), produced by spiniferous papillae (*SP*) contain brown pigment granules (*P*) and are distributed throughout the cuticle (*C*) at a density of about 2,500/mm². One spiniferous papilla has produced a stalked, reticulate nodule (*arrow*). Common epidermal cells (*CEC*) occur ubiquitously between the papillae. This section grazes the stalk of a spicule (*arrowhead*). The dermis (*DE*) contains a few artifactual wrinkles (*W*). × 440

Fig. 2. A scanning electron micrograph of the surface of the perinotum. The hairs occur at a density of about 5/mm². Each hair has a longitudinal groove (*GR*) oriented toward the midline of the animal. × 19

Fig. 3. Median longitudinal section through the base of a girdle hair. Common epidermal cells (*CEC*) line the pocket in which the trichogenous papilla lies. This section grazes the chitinous rod (*CR*) that lies behind the cortical groove (see Fig. 2). The continuity of the medulla (*ME*) and cuticle (*C*) is visible in this section (*double-headed arrow*). Individual fiber bundles (between *white arrows*), each probably produced by a single subcortical cell (*CC*), can be seen in the inner layer (*IC*), but not in the outer layer (*OC*) of the cortex. The proximal end of one medullary dendritic bundle (*arrowhead*) is emerging from the papilla. One nerve (*NE*) is emerging from the base of the papilla and entering the dermis (*DE*). × 1,120

Both 0.5 µm and 1.0 µm sections were stained with a 1% solution of Azure II and 1% Methylene Blue in 1% sodium borate (Richardson et al. 1960). Thin sections (60-90 nm) were picked up on Parlodion- and carbon-coated copper grids and stained with uranyl acetate and lead citrate. Grids were examined on a Philips EM 300 electron microscope. Specimens for scanning electron microscopy were fixed as for transmission work, dehydrated in ethanol and acetone and dried by the critical point method. Specimens were coated with carbon and gold-palladium, and examined with a JEOL JSM 35 microscope.

Thick sections of undecalcified tissue were viewed under a polarizing microscope. The sign of birefringence was determined with a first order red plate.

Results

General organization of the epidermis

A homogenous cuticle, about 100 µm thick, covers the dorsal epidermis of the perinotum of *Mopalia muscosa* (Figs. 1, 25). The presence of chitin in this layer and in hairs was determined by Campbell's method (1929). Calcareous spicules are embedded in the cuticle (Figs. 1, 25), but the hairs, up to 5.0 mm in length and ranging in diameter from 20 µm to 400 µm, grow through and beyond the surface of the cuticle (Figs. 2, 25). The epidermis is a simple epithelium composed mainly of cuboidal *common epidermal cells* (Figs. 1, 3, 6, 25). Small *spiniferous* and larger *trichogenous papillae* composed of columnar cells are distributed over this epithelium (Figs. 1, 25). Each trichogenous papilla secretes a hair and each spiniferous papilla produces one spicule (Figs. 1, 3, 25). Some spiniferous papillae also produce stalked nodules (Fig. 1), known as "morgensternformiger Körper" in the German literature (von Knorre 1925). Processes of pigment cells with green granules occur in the spiniferous and trichogenous papillae (Figs. 22, 24), and among the common epidermal cells (Fig. 6). The only cell bodies of pigment cells that we have found were in the dermis. The dermis is separated from the epidermal cells by a thick basal lamina (Fig. 24). Densely packed collagen fibers (Fig. 23), scattered muscle fibers, nerves (Fig. 8) and processes of pigment cells (Figs. 23, 25) compose the bulk of the dermal material.

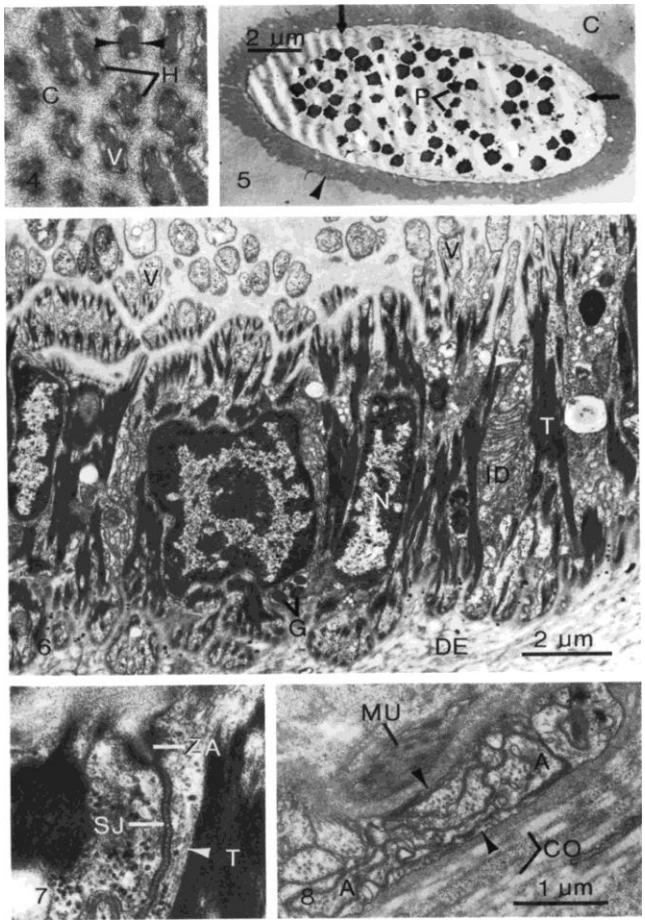


Fig. 4. A grazing section through the apical microvilli (*V*) of a common epidermal cell (compare with Fig. 6) demonstrates the dense bundles of tonofilaments (between *arrowheads*), which insert on hemidesmosomes (*H*). The granular cuticle (*C*) is visible between the microvilli. ×26,500

Fig. 5. A longitudinal section through a decalcified spicule. The pigment granules (*P*) are surrounded by a fibrous matrix (*arrows*) at sites that were occupied by the calcium carbonate crystals. An electron-dense material (*arrowhead*) surrounds each spicule and adjoins the cuticle (*C*). ×5,200

Fig. 6. A longitudinal section through the common epidermal cells. Dense bundles of tonofilaments (*T*) surround the nucleus (*N*) and extend from the bases to the apices of the cells. They anchor in the digitate, branching microvilli (*V*) and in the basal protruberances that project into the dermis (*DE*). The junctional complex (*arrowhead*) is like the one enlarged in Fig. 7. The lateral margins of the cells are extensively interdigitated (*ID*). Ovoid granules (*G*) in a process of a pigment cell occasionally occur among these cells. ×8,550

Fig. 7. Two common epidermal cells are joined by an apical zonula adhaerens (*ZA*) and a subjacent septate junction (*SJ*). Microtubules (*arrowhead*) are occasionally associated with the bundles of tonofilaments (*T*). ×60,000

Fig. 8. A transverse section of a dermal nerve. The axons (*A*) are irregular in shape and intertwined. The superficial cells (*arrowheads*) may be glial cells that ensheathe some of the axons. This nerve has no associated processes of pigment cells. ×17,900

Common epidermal cells

The apical surface of each common epidermal cell bears digitate, often branched, microvilli (Fig. 6). These cells are joined laterally, just below the apex, by zonulae adherentes and subjacent zonular septate junctions (Fig. 7). Adjacent cells are extensively interdigitated along their lateral surfaces. Each cell contains a large central nucleus and many free ribosomes. Dense fascicles of tonofilaments span the length of each cell and insert on apical and basal hemidesmosomes. Microtubules are irregularly associated with these fascicles (Figs. 4, 6, 7).

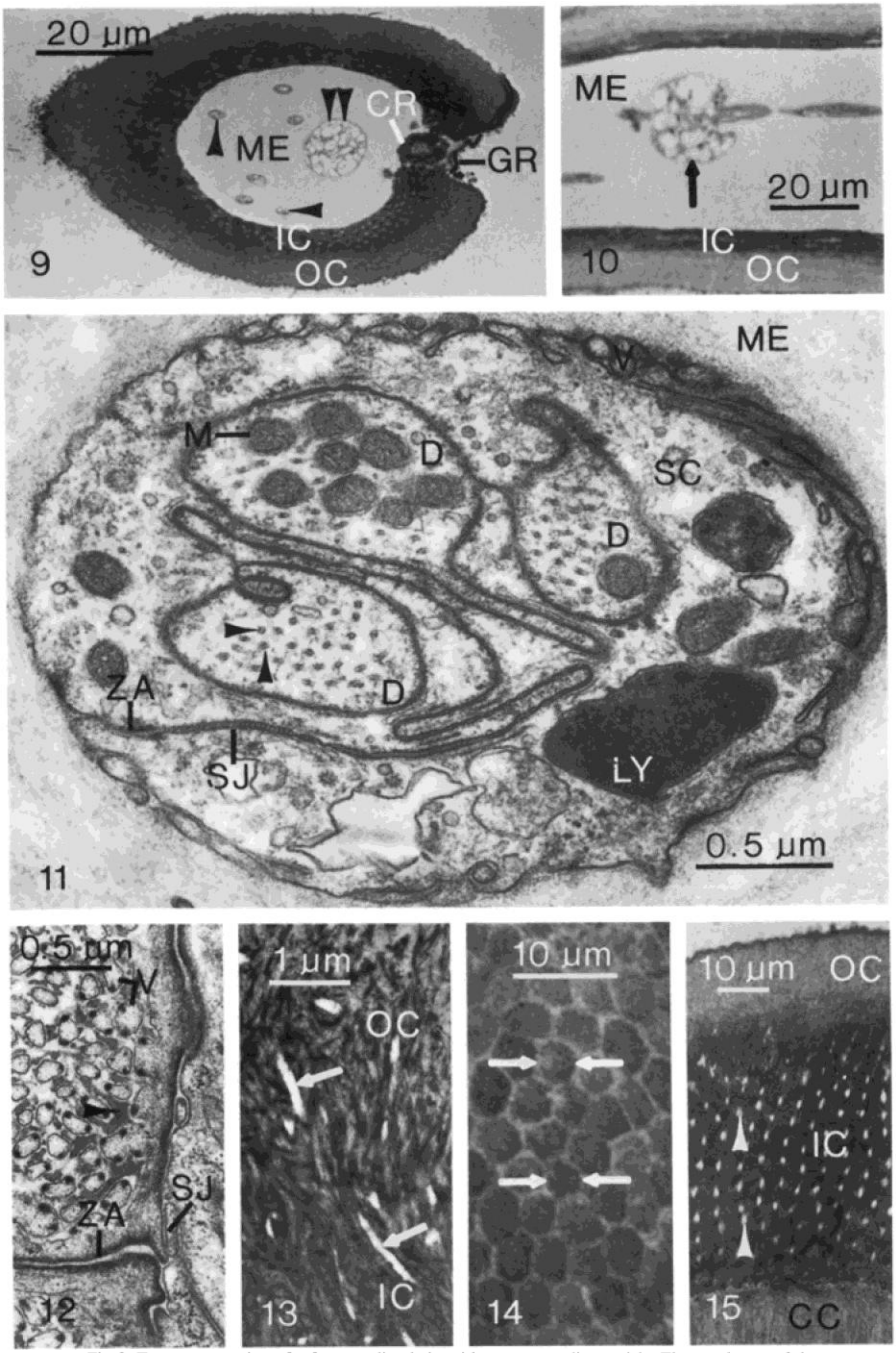


Fig. 9. Transverse section of a free-standing hair, with no surrounding cuticle. The two layers of the cortex (*IC, OC*) are less distinct here than they are nearer to the epidermis (Fig. 3). Seven dendritic bundles (*arrowheads*) lie in the medulla (ME). One bundle is swollen into a nodule (*double arrowheads*). The groove in the cortex (*GR*) exposes the medullary matrix to the environment. The cortical rod (*CR*) lies just to the inside of the groove. ×800

Fig. 10. Longitudinal section of a free-standing hair. One dendritic bundle bears a nodule (*arrow*). This swelling is continuous proximally and distally with typical dendrites and supporting cells. The inner (*IC*) and outer (*OC*) layers of the cortex are distinguishable in this section. ×630

Fig. 11. Transverse section through a medullary dendritic bundle. Three dendrites (*D*) are enclosed by a single supporting cell (*SC*). The dendrites have numerous parallel microtubules (*arrowheads*) and mitochondria (*M*). The supporting cell contains these organelles, small vesicles and lysosomes (*LY*). Short microvilli (*V*) occur on the surface of the supporting cell. The mesaxon of the supporting cell is joined by a zonula adhaerens (*ZA*) and a septate junction (*SJ*). ×37,200

Fig. 12. Grazing transverse section through the apical field of microvilli (*V*) of some subcortical cells. Zonulae adhaerentes (*ZA*) and septate junctions (*SJ*) join these cells. Electron-dense glycoprotein of the hair cortex (*arrowhead*) surrounds the microvilli. ×22,600

Fig. 13. Grazing section through the hair shaft at the junction of the inner (*IC*) and outer (*OC*) cortex. Apical microvilli on the subcortical cells probably occupy the electron-lucent channels (*arrows*). ×11,600

Fig. 14. Grazing section through the base of the inner cortex. Each fibrous bundle (between *arrows*) is probably produced by one subcortical cell. ×1450

Fig. 15. Grazing section through the cortex and adjacent subcortical cells (*CC*). Individual fibrous bundles are visible in the inner cortex (*IC*). The light channels (*arrowheads*) are the interstices between adjacent bundles. ×690

Spicules

Within the dorsal cuticle are fusiform spicules, approximately 36 μm in length and 12 μm in diameter (Fig. 1). Each spicule consists of a central mass of brown pigment granules and a peripheral layer of calcium carbonate crystals (Figs. 1, 5, 25). A layer of electron-dense cuticular material surrounds each spicule (Fig. 5). This material tapers basally to form a stalk. The base of the stalk adjoins the apices of several cells in the spiniferous papilla. When we examined thick, free-hand sections of the integument with a polarizing microscope, we found that the spicules are negatively birefringent when their long axes are parellel to the slow axis of a first order red plate. The birefringence disappears if the material is treated with EDTA or 1N HC1. These observations support previous assumptions that the spicules contain oriented calcium carbonate crystals (Leloup 1942).

Some spiniferous papillae produce stalked nodules (Fig. 1) that are embedded in the cuticle. The periphery of the nodule contains large vacuoles. The stalk appears to contain neurites. Further work is necessary to clarify the relationship of these neurites to the papillary cells.

The spicules on the ventral surface of the girdle lack pigment granules and are larger than the dorsal spicules. A comparison of these two structures and the underlying papillae will be the subject of a future paper.

Girdle hairs: Extracellular components

The girdle hairs of *M. muscosa* are curved, distally tapered, chitinous structures (Fig. 2). The shaft of each hair is composed of a bilayered cortex and a central medulla (Figs. 3, 9, 25). The cortex is interrupted by a longitudinal groove that extends the entire length of the shaft on the mesial surface (Figs. 2, 9). A discrete rod of cortical material, 12.0 to 17.0 μm in diameter, lies within the gap in the cortex (Fig. 9). The medullary matrix surrounds the cortical rod and is continuous with the cuticle (Fig. 3). Above the cuticle, the longitudinal groove exposes the medullary matrix to the external environment (Figs. 2, 9). Chitinous fibers in the inner cortex are aligned in bundles that lie parallel to the long axis of the hair (Figs. 3, 25). These bundles form a dense field that is interrupted by longitudinal channels, approximately 1.0 μm in diameter (Fig. 15). These channels, of low density, are the interstices between adjacent fibrous bundles. Each bundle contains smaller, electron-lucent tracts of various widths (Fig. 13). The inner cortex contains more electron-dense fibers than the outer layer (Figs. 3, 13) and stains more intensely in 1.0 μm sections. The entire cortex is strongly birefringent.

The cortical rod is also bilayered. The center of the rod stains lightly in 1.0 μm sections and resembles the outer cortex of the hair (Fig. 9). Fibrous bundles, resembling those in the inner cortex, completely surround the lightly staining center of the cortical rod (Fig. 9).

Girdle hairs: Cellular elements of the trichogenous papilla

All the cells of a trichogenous papilla are columnar and uninucleate, but the position of the nucleus along the apical-basal axis varies in different cells. The cells at the base of the medulla, the submedullary cells, form a hillock which protrudes into the medullary matrix beyond the level of the apices of the cortical cells (Fig. 3).

Each subcortical cell, at the base of the cortex, apparently produces one bundle of chitinous fibers (Fig. 14) and bears 150-200 long, wavy, apical microvilli (Figs. 12, 16). We infer that the small electron-lucent areas in each fibrous bundle are channels left by the apical microvilli (Fig. 13). The junctional complexes between these cells are similar to those joining the common epidermal cells (Fig. 7). Subcortical cells contain a few multivesicular bodies and extensive rough endoplasmic reticulum with a moderately electron-dense matrix in the slightly enlarged cisternae. The Golgi apparatus also contains electron-dense material in its saccules and vesicles (Fig. 16).

The submedullary cells are the longest in the papilla and are extensively interdigitated, both laterally and basally (Figs. 22, 24). These cells have abundant rough endoplasmic reticulum, many free ribosomes, glycogen, mitochondria, many secondary lysosomes, a few multivesicular bodies, and supranuclear Golgi bodies (Fig. 19). These cells bear short apical microvilli (Fig. 19).

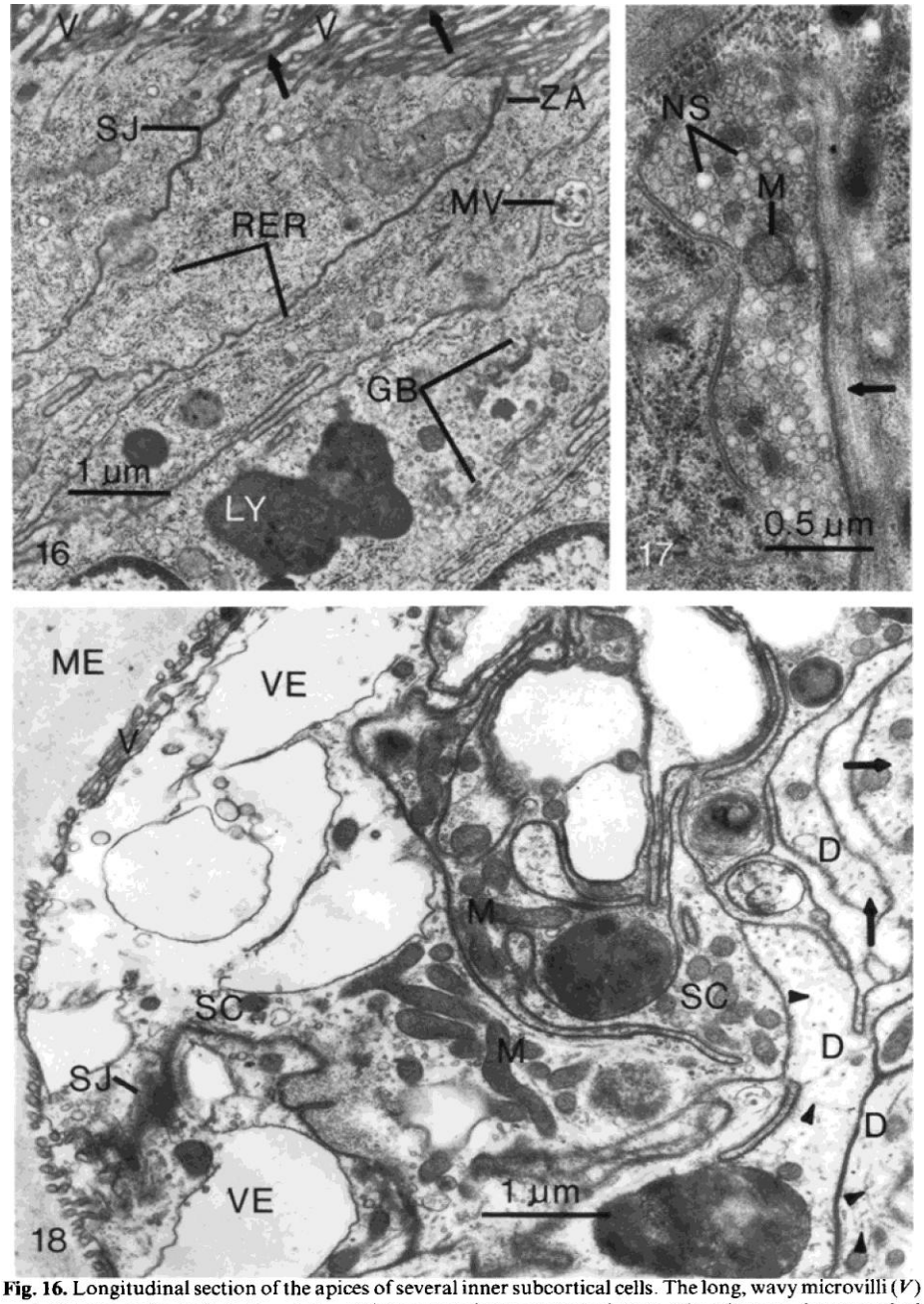


Fig. 16. Longitudinal section of the apices of several inner subcortical cells. The long, wavy microvilli (*V*) probably leave channels in the cortex which remain in the hair shaft (Fig. 13). Electron-dense cortical material (*arrows*) occurs between the microvilli. The cisternae of the rough endoplasmic reticulum (*RER*) and the saccules and vesicles of the Golgi apparatus (*GB*) contain electron-dense material. ×13,400

Fig. 17. A putative presynaptic terminal at the base of a trichogenous papilla. 50–70 nm light-cored vesicles (*NS*) are visible. The adjacent nerve, cut in a grazing section, has longitudinal profiles of microtubules (*arrow*) and may be the post-synaptic terminal. ×30,200

Fig. 18. Section through part of a reticulate nodule (Figs. 9, 10) along a medullary dendritic bundle. The dendrites (*D*) entering this nodule have lost their typical organization; the dendritic mitochondria are twisted, the microtubules are no longer in parallel arrays (*arrowheads*) and smooth vesicles (*arrows*) appear in the axoplasm. Large electron-lucent vacuoles (*VE*) lie around the periphery within the supporting cells (*SC*) of the nodule. Stubby microvilli (*V*) line the margin of the supporting cells next to the matrix of the medulla (*ME*). ×17,400

Girdle hairs: Innervation

The medulla may contain as many as 20 parallel bundles of dendrites that extend from the apices of the submedullary cells and terminate near the tip of the hair (Figs. 3, 9). Each bundle terminates at a different level within the hair shaft; only a few reach the tip. The width of the cortex decreases near the tip of the hair and the dendrites end bluntly within the medulla. The medulla normally covers the dendrites, but they may be exposed to the environment if the tip of the hair is eroded. The medullary dendritic bundles range in diameter from 1.8 µm to 5.7 µm, and contain from 1 to 25 dendrites surrounded by processes of one or two epidermal supporting

cells (Fig. 11). The dendrites are produced by epidermal sensory cells (Figs. 19, 25). Several sensory cells contribute to each bundle of dendrites. The dendrites emerge from the apices and subapical margins of the sensory cells. Each bundle may contain several dendrites from a single sensory cell. Large hairs have more bundles of dendrites than small hairs and large dendritic bundles contain more dendrites than small bundles. Longitudinally oriented neruotubules, mitochondria and a few small vesicles occur throughout the dendrites. One or two epidermal supporting cells adjacent to the sensory cells form the sheath that surrounds the dendrites (Figs. 11, 19). Processes of the supporting cells contain numerous vesicles, many mitochondria, multivesicular bodies and large lysosomes. Only a few microtubules occur in these processes. The surfaces of the supporting cells adjacent to the medullary matrix are studded with microvilli, similar to those on the apices of the submedullary cells (Figs. 11, 19). Mesaxons are formed by single supporting cells. A superficial zonula adherens and a subjacent septate junction join the outer mesaxon in these cases. Similar junctional complexes join the supporting cells of dendritic bundles with two supporting cells.

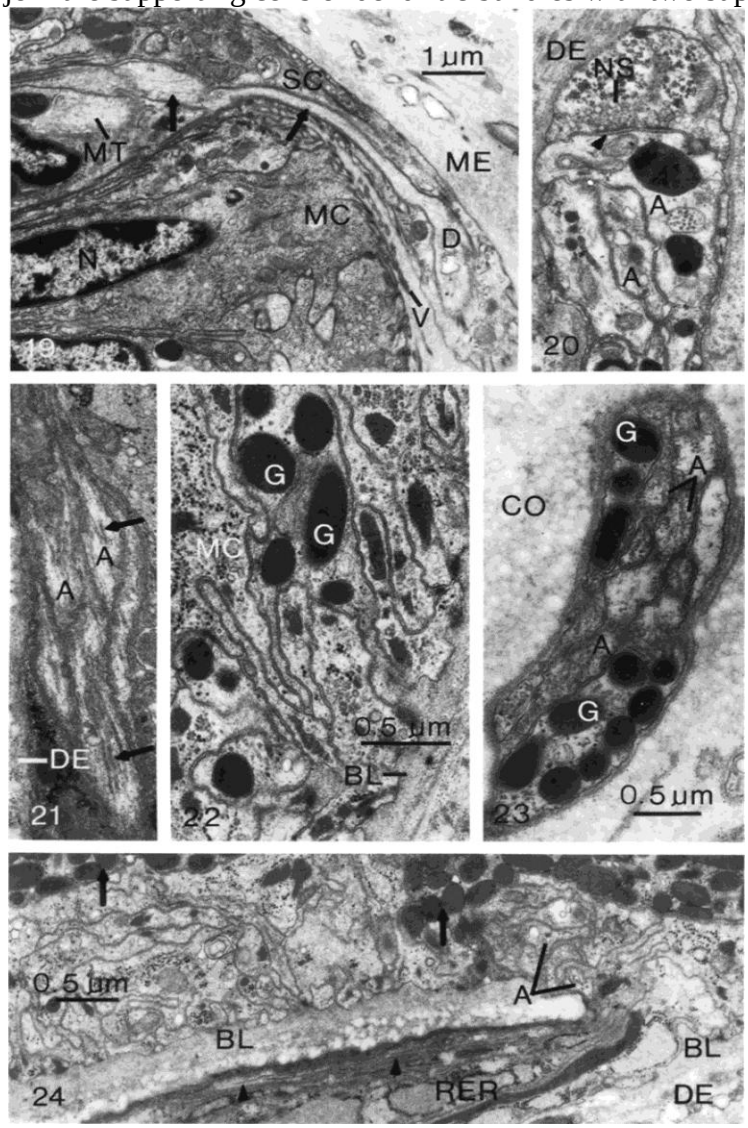


Fig. 19. Grazing section through the tips of some submedullary cells (*MC*). One dendrite (*D*) is emerging from the apex of an epidermal sensory cell. Parallel microtubules (*arrows*) occur in this dendrite. A similar array of microtubules (*MT*), next to the nucleus (visible at the left margin of the micrograph), occurs in an adjacent sensory cell that also produces a dendrite (out of the plane of this section). ×9,850

Fig. 20. Grazing section through part of a dermal nerve that emerges from a trichogenous papilla. The pre-synaptic terminal has thickened membranes, contains 50-nm neurosecretory vesicles (*NS*) and is separated from the post-synaptic cell (*A*) by a 35 nm cleft (*arrowhead*). ×20,900

Fig. 21. Enlargement of the dermal axons (see Fig. 24, *arrowheads*) in a section adjacent to that in Fig. 24. The orientation is perpendicular to that in Fig. 24. Five axons (*A*) have longitudinal arrays of microtubules (*arrows*) and few other organelles in this grazing section. ×27,500

Fig. 22. Grazing section through the base of a trichogenous papilla. Processes of pigment cells containing membrane-bound, ovoid pigment granules (*G*) occur between the submedullary cells (*MC*). ×29,500

Fig. 23. Dermal nerve with several axons (*A*). Processes of cells with ovoid pigment granules (*G*) like those in the epidermis (see Fig. 22) occur alongside the axons. Collagen fibers in transverse section (*CO*) fill much of the dermis. ×22,500

Fig. 24. Grazing section through the base of a trichogenous papilla showing an emerging nerve. Axonal profiles (*A*) are visible in the papilla above the basal lamina (*BL*) and in the dermal nerve (*arrowheads*) (see Fig. 21). It is not clear whether the profiles of the rough endoplasmic reticulum (*RER*) are in glial cells or axons. The isolated areas with large ovoid granules (*arrows*) have been followed in serial thin sections and are extensions of a single pigment cell. Note extensive interdigitation between the epidermal cells. ×19,500

Each medullary dendritic bundle enlarges into a reticulate nodule at a variable level above the cuticle (Figs. 9, 10). In these areas the dendrites appear swollen (Fig. 18). The neurotubules are no longer parallel; numerous small vesicles, mitochondria and lysosomes are present. In the nodules the supporting cells contain large peripheral vacuoles. Above the nodules, the dendrites and supporting cells retain their characteristic structure (Fig. 10). In most hairs, the cells below the cortical rod also form a similar reticulate nodule.

Nerves with and without processes of pigment cells occur throughout the dermis (Figs. 8, 23). Several nerves traverse the basal lamina and join the base of each papilla (Figs. 3, 21, 24). Most of these fibers are probably

afferent but some may be efferent. We have been unable to find connections between epidermal cells and these basal papillary nerves. Profiles of fibers with neurosecretory vesicles were found in the bases of papillae (Fig. 17). One hair with 5 medullary dendritic bundles had 5 separate, putative presynaptic terminals near the base of the papilla. These terminals contained light-cored (50-70 nm) vesicles. A few papillary nerves were traced across the basal lamina into the dermis. Synapses were found among the dermal neuronal processes (Figs. 20, 24).

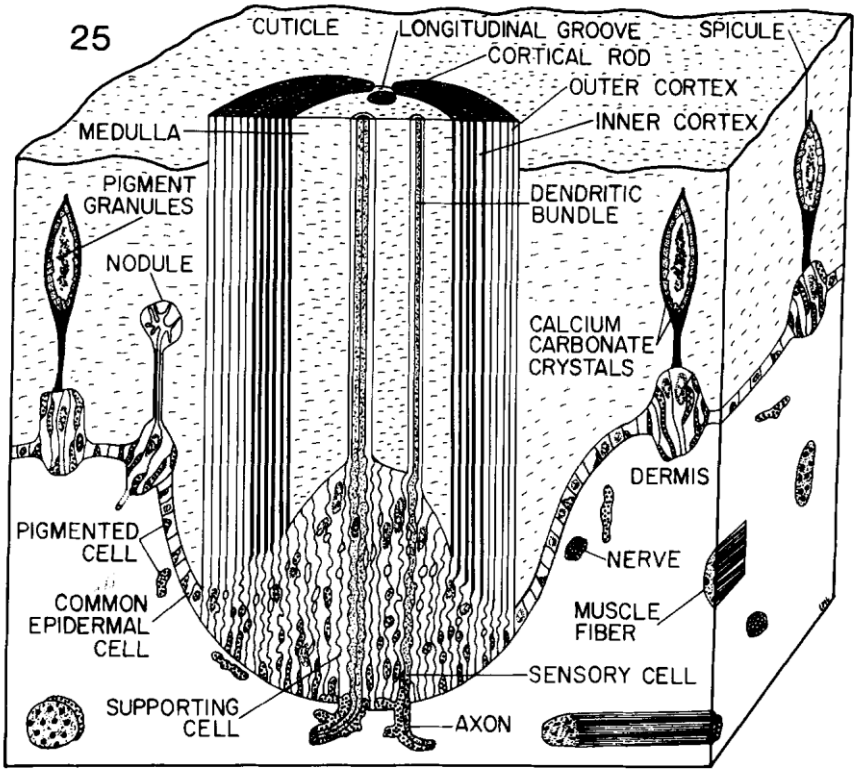


Fig. 25. A diagrammatic representation of the epidermis of *M. muscosa*. The spicules, produced by spiniferous papillae, are embedded in the cuticle and contain brown pigment granules surrounded by calcium carbonate crystals. A spicule is surrounded by a layer of dense cuticular material and remains connected to the cells of a papilla by a stalk. Some of the spiniferous papillae produce stalked nodules. Because preliminary observations have shown that neurites occur in these nodules, putative axons are diagrammed as emerging from this type of papillae. One hair, secreted by a trichogenous papilla, in an epidermal invagination, contains two dendritic bundles. The dendritic bundles are stippled because the dendrites are not parallel tubes. Two nerves are shown emerging from the base of the papilla. Processes of pigment cells occur among the epidermal cells and in the dermis. Many of these processes, as diagrammed here, adjoin the papillary axons and the dermal nerves and muscle fibers

Processes of pigment cells occur between the epidermal cells around the base of each papilla. These processes contain arrays of parallel microtubules, mitochondria, free ribosomes and many homogenous, membrane-bound, ovoid, pigment granules, approximately 190-400 nm in width and 430-830 nm length (Figs. 22, 24). Similar processes occur in the dermis adjacent to the papillae (Fig. 23). In vivo, the granules are bright green.

Discussion

Girdle hairs: Morphological evidence for a sensory function

In chitons, epidermal sensory receptors have been found around the mouth, on the subradular organ, in the buccal cavity, in the pallial grooves and in the shell (Moseley 1885; Hyman 1967; Boyle 1975; 1977). The girdle hairs of *Mopalia muscosa* do not resemble any of these sensory organs. All of the molluscan chemoreceptive (Demal 1955; Graziadei 1964; Barber and Wright 1969; Crisp 1971, 1973; Wright 1974a, b; Laverack 1974; Emery 1975a, b; Emery and Audesirk 1978; Benedeczky 1979) and mechanoreceptive neurons (Santer and Laverack 1971; Santi and Graziadei 1975; Graziadei and Gagne 1976; Moir 1977) that have been described, have specialized dendritic endings that are exposed to the environment. Unlike these dendrites, the dendrites in chiton hairs are enclosed within a chitinous hair shaft.

The dendrites in chiton hairs have no microvilli or cilia and are ensheathed by processes of supporting cells. The mesial groove exposes the medulla to the environment, but we have resolved no pores in the medulla. If the chiton hairs are specialized chemosensory devices, molecules would have to pass through the chitinous medulla as well as the supporting cells to make contact with the dendritic membranes. The medulla may be permeable to small molecules, but unless the supporting sheath cells are sensory, it is unlikely that the chiton hairs are specialized chemoreceptors.

Except for terminal membrane specializations, the medullary dendrites in *M. muscosa* resemble the neurites in the aesthetes of *Lepidochitona cinereus* (Boyle 1974), the dendrites in the metapodial tentacles of *Nassarius reticulatus* (Crisp 1971) and the dendrites in the tentacles of the pulmonate *Anion ater* (Wright 1974b). Although all previously described molluscan sensory neurons have terminal cilia or microvilli, we have found no cilia, stereocilia or microvilli in the medullary dendrites in the chiton hairs.

The presence of secondary sensory cells, without axons, such as those found in the taste buds of vertebrates and the acousticolateralis system (Bullock et al. 1977), has not been demonstrated in the Mollusca. Both Crisp (1971) and Zylstra (1972) dispute a claim by Storch and Welsch (1969), of finding secondary receptors in some prosobranchs. Several nerves emerge from the base of each trichogenous papilla in *Mopalia muscosa.* If the epidermal sensory cells are primary bipolar neurons, then some of the fibers in these nerves should be axons that emerge from the sensory cells. Because we were unable to trace processes from the trichogenous sensory cells to the basal papillary nerves, we could not determine whether the sensory cells are primary neurons or secondary sensory cells.

The number of basal nerves associated with each papilla is variable. We do not know the ratio of medullary dendritic bundles to basal papillary nerves in any hair, but each basal nerve contains several axons and each papilla may have several basal nerves. There appear to be enough axons emerging from each trichogenous papilla to account for one axon from each sensory neuron. Some of the axons could be inhibitory or excitatory fibers which originate in the central nervous system.

The function of the reticulate nodules (Figs. 10, 18) in the medullary dendrites is unknown. The swollen dendrites contain aggregations of mitochondria, as do the dendritic swellings of the frontal filament complex of larval barnacles, according to Walker (1974), who suggested that the mitochondria provide energy needed to transport ions across the membranes of the ciliary projections in the frontal filaments as part of a pressure reception system. The nodules in *M. muscosa* may have a similar function.

Functions of the integument

The function of the polyplacophoran girdle integument is not well understood. Although girdle structures have been deemed armature (Pilsbry 1892; Hyman 1967), tests are needed to determine if the girdle integument of any species actually deters potential predators. The overlapping scales of some species may retain water during low tides, helping the animal to avoid desiccation. The hairs of *M. muscosa* entrap mud and detritus and often support an extensive epiphytic and epifaunal community (Phillips 1972). This may also benefit the chiton during low tides. Because the basal "spicule-forming" cell in *Lepidochitona cinereus* has a neurite-like process, Haas and Kriesten (1975) suggested that the spicules may be mechanoreceptors. Fischer et al. (1980) have stated that the spicules in *Acanthochiton fascicularis* are tactile, and that the spiniferous papillae of *A. fascicularis* also contain "visual" cells, but the innervation of these structures has not been described.

Adult chitons respond when the hairs are bent or pinched. Following stimulation of the hairs, the animals show a "clamping" response and tighten their hold on the substratum (E. M. Leise, unpubl.). If a few hairs are bent, the animals will move in the opposite direction. The possibility that these animals were responding to deformations of the skin could not be eliminated.

Pigment cells and the "gliointerstitial system" of molluscs

Processes of pigment cells occur in both the dermis and the epidermis of *M. muscosa.* The morphology of the granules in these cells, the occurrence of the cellular processes alone in the dermis and in association with dermal nerves and muscles, and the rare occurrence of the cell bodies, suggests that these are homologous with the gliointerstitial cells found in many other molluscs (Nicaise 1973). Nicaise claims that typical granules in gliointerstitial cells are not colored, but the high density of these cellular processes in and below the epidermis in *M. muscosa* may have allowed us to see their hue.

A comparison of chiton hairs and invertebrate setae

The setae of larval polychaetes (Gustus and Cloney 1973), echiuroids (Orrhage 1971), larval brachiopods (Gustus and Cloney 1972) and pogonophorans (George and Southward 1973) are small, rigid structures with basal diameters between 1.0 and 2.0 μm. The setae of juvenile nereid polychaetes are 30.0 μm in diameter (Gustus 1973), the same size as small chiton hairs. Chiton hairs are similar to these setae because the subcortical cells have long apical microvilli, as do the chaetoblasts of the polychaetes and brachiopods. These microvilli are probably involved in orienting the glycoprotein within the hair. A single chaetoblast governs the architecture of a seta, but the position of the cortex and medulla are probably controlled by the different populations of cells within the multicellular trichogenous papilla.

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